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"DISTANCE EFFECT" IN PIGEON ORIENTATION: AN EVALUATION

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In several papers, Matthews (1955, 1963) has reported that his pigeons exhibit poorer orientation when released at intermediate distances than when released at very short distances or at long distances. He interprets this "distance effect" as indicating that the pigeons' system of navigation is not sufficiently accurate to be used effectively at distances less than about 80 km. Matthews explains the accurate vanishing bearings of his pigeons at very short distances as probably being due to pilotage by familiar landmarks rather than to true navigation. He suggests that at intermediate distances the birds are too far from home to use landmarks but still too close to use accurately their bicoordinate navigation system, hence their poor homeward orientation.

Mittelstaedt (*in* Schmidt-Koenig, 1963a, 1963b) examined orientation as a function of distance in terms of the homeward component (*i.e.,* the component of the mean vanishing vector that is in the homeward direction), but the results of his analysis of the initial orientation of naive pigeons in Germany were inconclusive. An analysis by Schmidt-Koenig (1965, page 244) of the orientation of Matthews' experienced pigeons in England provided no convincing evidence of a distance effect, nor was convincing support for such an effect obtained in an elaborate series of releases conducted by Schmidt-Koenig (1963) in North Carolina. Later, however, Schmidt-Koenig conducted extensive tests of the distance effect in experienced pigeons flown in both North Carolina (1964, 1966) and Germany (1968), and published results that seemed to support Matthews' ideas. He found high values of the homeward component at distances less than about 19 km and greater than about 96 km; between these distances there was a zone of poor orientation. Wallraff (1967) reported similar results with untrained pigeons released on their first homing flights in Germany.

If the distance effect is a general characteristic of pigeon homing, it has important implications for the nature of the navigation system used by these birds. It would be consistent, for example, with a system such as the sun-arc hypothesis of Matthews (1953), which would be effective at short distances only if the birds could determine the sun's position with far greater precision than most workers have believed possible. Matthews (1968) has recently relied heavily on the distance effect in interpreting much of the published data on pigeon homing.

Because of the theoretical importance of the distance effect if it really exists, and because I have doubted its general occurrence in view of the very good homeward orientation regularly exhibited by both our untrained (Keeton and Gobert, 1970) and our experienced (Keeon, 1969) pigeons at the intermediate distances where orientation should be poorest, my colleagues and I conducted, during 1968 and 1969, an extensive series of test releases to determine whether any distance effect is evident in the performance of our pigeons.

Methods

Test releases were performed at various distances north, east, south, and west of the Cornell pigeon lofts at Ithaca, New York. More particularly, the release sites were: North—5.9, 10.0, 26.8, 49.0, 84.6, 143.3, 200.3 km; East—5.7, 14.9, 33.5, 60.9, 91.1, 129.8, 164.2, 204.2 km; South—5.4, 12.1, 20.5, 32.6, 47.3, 49.5, 84.5, 124.6, 188.3 km; West—9.0, 17.8, 33.9, 47.2, 70.3, 119.9, 155.9, 177.7 km. At all but the most distant sites, a minimum of three test releases (usually more) were conducted, using different birds, and on different days. Except in 12 instances, at least 10 single-tossed birds (mean = 14.7) were used in each test release. Included in the analysis reported here are the results of a total of 172 test releases involving a total of 2525 single tosses of birds.

All birds used in the test releases had had previous homing experience from all four cardinal directions. For releases at 20 km or less, the birds' previous experience had included single-toss flights from distances this great or greater. For releases at more distant sites, the birds had previously made single-toss flights from distances at least as great as that of the next nearer site in the series.

In each test release, the birds were tossed individually from the hand, the directions in which they were pointed at the toss being randomized. Each bird was observed with 10 × 50 binoculars until it vanished from sight, and a compass bearing for the vanishing point was recorded to the nearest 5 degrees. The interval between toss and vanish was timed with a stop watch. No bird was released until the previous bird had been out of sight at least 5 minutes.

The circular mean (both direction and vector length) of the vanishing bearings of each release was calculated by vector analysis, following the procedure outlined by Batschelet (1965). Bearings were tested for randomness by means of the Rayleigh test (Batschelet, 1965). The homeward component was calculated as proposed by Mittelstaedt (*in* Schmidt-Koenig, 1963a, 1963b): $h = a \cdot \cos(\alpha - \beta)$, where a is the length of the mean vector, α is the mean direction, and β is the home direction. The homeward directional component was calculated by the equation: $d = \cos(\alpha - \beta)$. Values for both the homeward component and the homeward directional component may range from -1 to $+1$; values for the length of the mean vector may range from 0 to $+1$.

For each of the four directions, the homeward component (HC), homeward directional component (HDC), and length of mean vector (LMV) were plotted as a function of the distance of the release sites from the loft. In each case, the curves are based on the arithmetic means of the corresponding values obtained from all tests at each site.

Since it seemed possible that the length of the vanishing intervals (elapsed time between toss and vanish) might indicate something about the relative difficulty of orienting at different release sites, the mean vanishing interval for each release was calculated, and then the means of the means for all tests at each site were plotted as a function of distance.

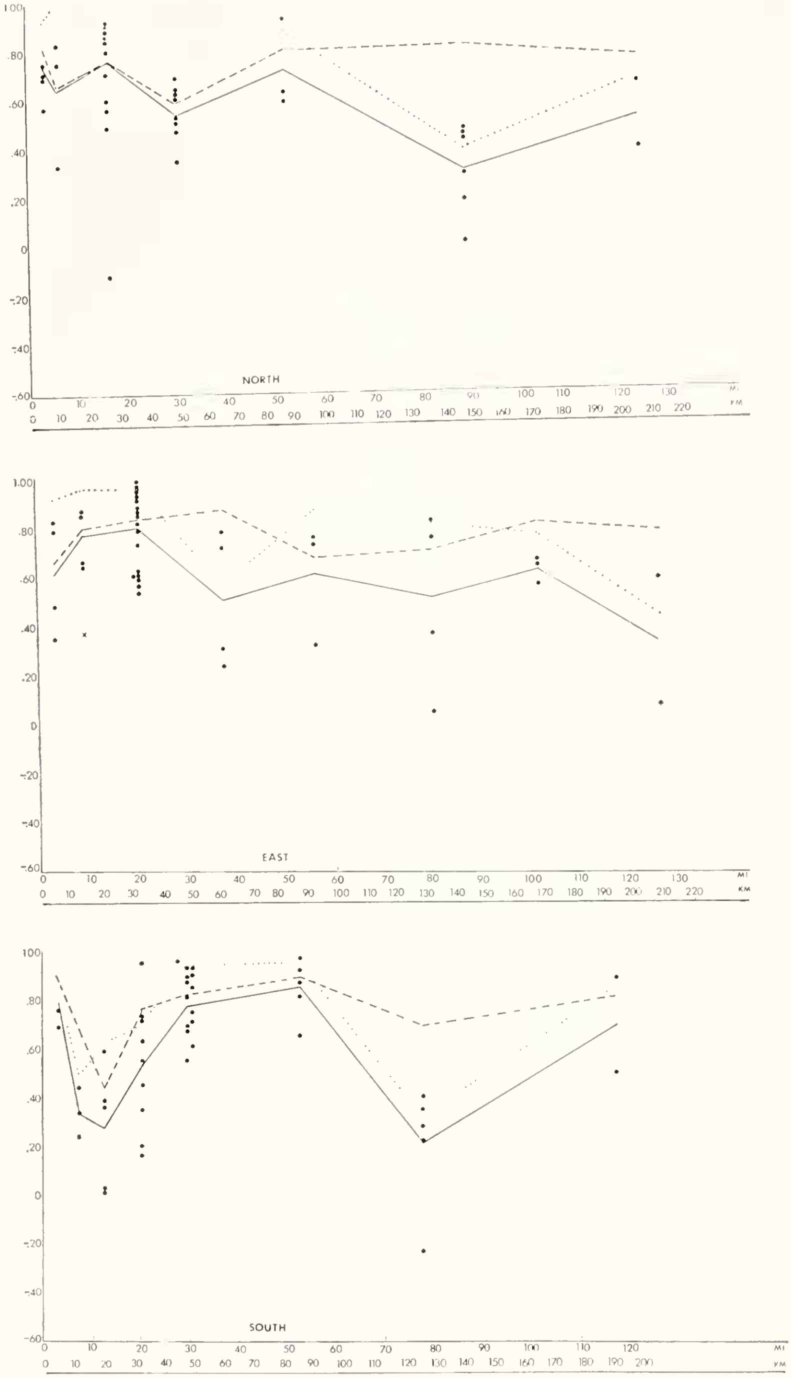
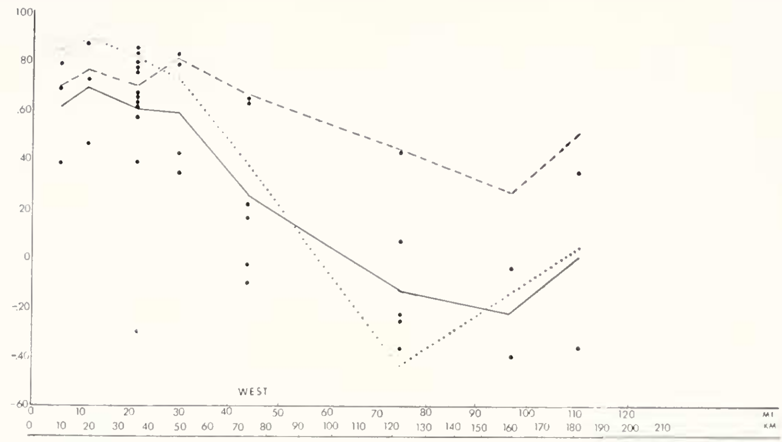


FIGURE 1, A–C.



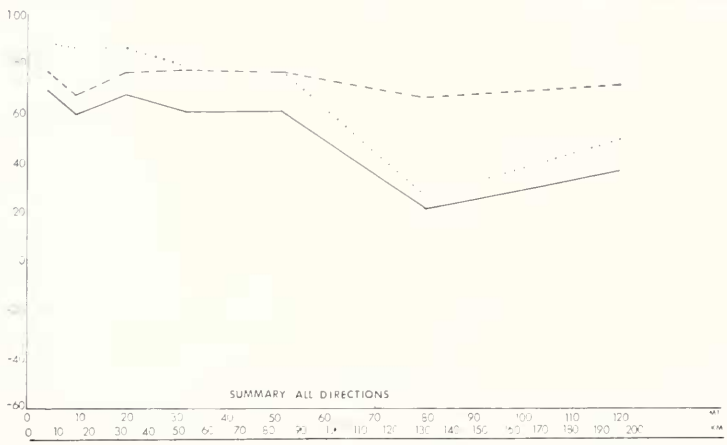


FIGURE 1. Graphs of the homeward component (solid curves), homeward directional component (dotted curves), and length of mean vector (dashed curves) plotted against distance of release from the home loft. The black dots indicate the values of the homeward component for the individual test releases; the curve connects the arithmtic means of the values for each site; A, releases from north of the loft; B, releases from the east; C, releases from the south; D, releases from the west; E, summary of all releases. The value indicated by X at 15.1 km in graph B is the mean homeward component for five releases at the alternate site discussed in the text.

RESULTS

Figures 1A, 1B, 1C, and 1D show the results of our releases from north, east, south, and west of the Cornell lofts, respectively. Figure 1E is a graph of the results of averaging the values from the four directions.

Not only do our graphs of the homeward component show little resemblance to those based on Schmidt-Koenig's data, but also they show few resemblances among themselves. There is no indication that the homeward component varies consistently as a function of distance in the manner suggested by Matthews, Schmidt-

Koenig, and Wallraff. More specifically, the poor orientation reported by those authors for intermediate distances is not seen—indeed the average of the homeward components for 27–34 km (17–21 miles) is 0.67, a remarkably high value; it is difficult to imagine that significantly better orientation could be obtained consistently at any distance.

That the good orientation at intermediate distances shown by the experienced birds used in the graphed releases is not simply a result of training is demonstrated by the equally good orientation at these distances regularly exhibited by our first-flight pigeons. Figure 2 shows examples of typical releases of such birds at roughly

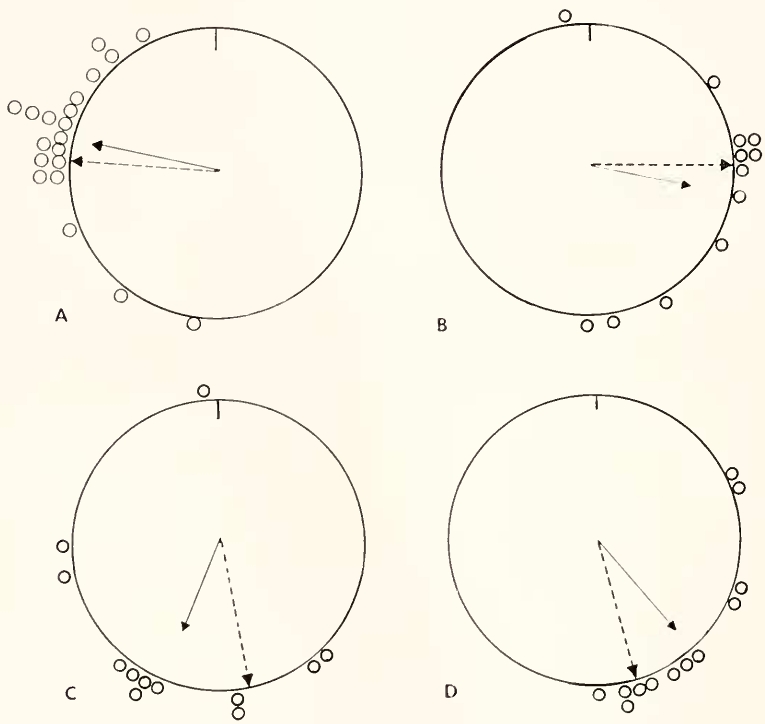


FIGURE 2. Examples of vanishing bearings of first-flight pigeons (ones never before taken away from the loft) released under sunny conditions: A, Harford, New York, 9.4 miles from the loft, April 25 and May 5, 1969, home bearing 276°, mean bearing 283° (nonrandom, $P < 0.0001$); B, Burdett, New York, 21.1 miles, October 23, 1968, home bearing 91°, mean bearing 101° (nonrandom, $P = 0.002$); C, near Locke, New York, 16.6 miles, October 23, 1968, home bearing 171°, mean bearing 205° (nonrandom, $P = 0.005$); D, Fleming, New York, 30.4 miles, December 12, 1968, home bearing 164°, mean bearing 139° (nonrandom, $P = 0.0007$). [In this figure and in Figures 4 and 5, the home direction is indicated by a dashed arrow, true north by a thin line at the top of the circle, and the mean vector by a solid arrow whose length is inversely proportional to the extent of scatter (the arrow would reach the periphery of the circle if there were no scatter, *i.e.*, if all the birds vanished in exactly the same direction, and the arrow would have 0 length if the vanishing bearings were uniformly scattered around the compass). Each symbol on the periphery of the large circle represents the vanishing bearing of one bird.]

16, 32, and 48 km (10, 20, and 30 miles); other examples have been published elsewhere (Keeton and Gobert, 1970).

Figure 3 shows mean vanishing intervals plotted against distance. The curves for the four cardinal directions show few resemblances among themselves. Except that for all directions vanishing intervals tend to be short at near (4–20 km) release points, there is no consistent relationship between vanishing interval and distance. In this regard, our results agree with those of Schmidt-Koenig (1966).

Discussion

In the published studies of distance effect, only the homeward component has been used as a measure of orientational performance. But the homeward component is not a particularly good measure since it is sensitive both to the deviation of the mean vector from the true home direction and to the extent of scatter of the bearings. Thus a homeward component of 0 could result from many fundamentally different distributions of the vanishing bearings, including two extreme distributions that are the opposites of each other—a circularly uniform distribution (*i.e.*, one with no mean vector) or a distribution in which all bearings deviate 90° in the same direction from home (*i.e.*, one as different from circular uniformity as a distribution can possibly be, but with the mean vector oriented at right angles to home). Clearly these distributions would have very different biological meanings, yet the homeward component permits no distinction between them.

Because of the desirability of distinguishing between the effects of mean directional error and the effects of scatter, the graphs in Figure 1 show, in addition to

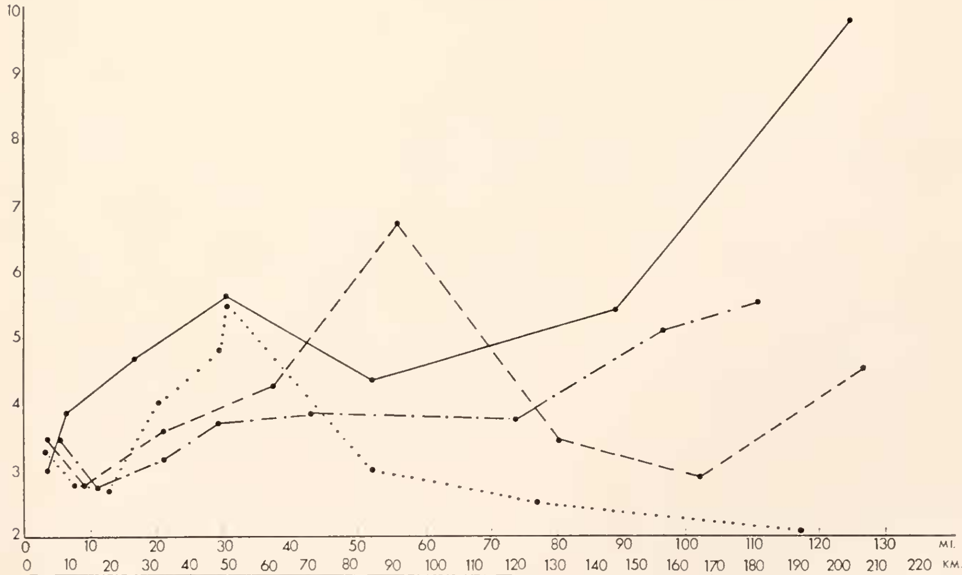


FIGURE 3. Graph of mean vanishing intervals (in minutes) plotted against distance of release from the home loft; North, solid curve; East, dashed curve; South, dotted curve; West, dot-dashed curve.

the homeward component, the homeward directional component and the length of the mean vector. The homeward directional component is a function only of the deviation of the mean vector from the home direction, and the length of the mean vector is a function only of the extent of scatter of the bearings. Hence these two indices give independent measures of the two variables that together determine the homeward component.

The figures indicate that the homeward directional component and the length of the mean vector vary independently. Thus, in Figure 1A it can be seen that the rises and falls of the homeward component curve at the shorter distances are due almost entirely to variations from site to site in the degree of scatter of the bearings, the accuracy of the mean bearings remaining nearly constant, whereas at the longer distances the shape of the curve is determined by variations in the accuracy of the mean bearings, the degree of scatter remaining nearly constant. In

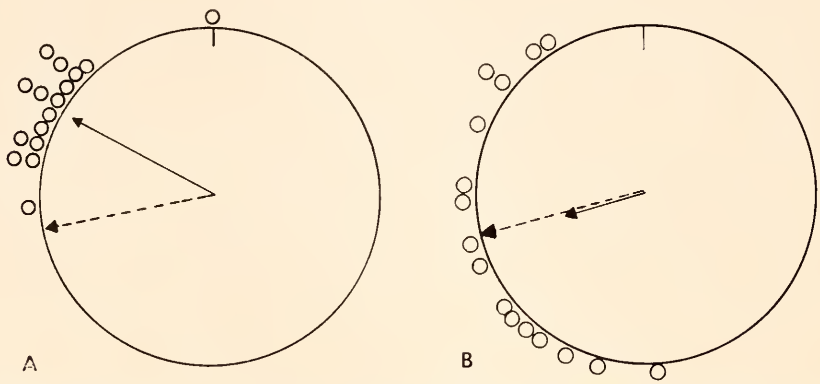


FIGURE 4. Release (A) showing very little scatter of the vanishing bearings but a mean deviating appreciably from the home direction, contrasted with a release (B) with much more scattered bearings but a more homeward directed mean; A, Berry Hill Fire Tower, New York, 37.9 miles from the loft, October 14, 1968, home bearing 258°, mean bearing 299° (nonrandom, $P < 0.0001$); B, near New Berlin, New York, 56.6 miles, July 30, 1967, home bearing 257°, mean bearing 256° (nonrandom, $P < 0.0001$).

Figure 1B, the similar values for the homeward component at the release sites 61 km and 91 km from the loft obscure the fact that at the 61 km site the mean vector deviates considerably from the home direction (mean HDC = 0.56) but the scatter of the bearings is minimal (mean LMV = 0.87), whereas at the 91 km site the mean vector is oriented very accurately toward home (mean HDC = 0.86) but the scatter of the bearings is greater (mean LMV = 0.67); *i.e.,* the similar values for the homeward component at the two sites result from quite different behavior by the pigeons (Fig. 4). Similarly, a sharp drop in the value of the homeward component is seen at both the 143 km north site (Fig. 1A) and the 120 km west site (Fig. 1D), but the behavior of the pigeons at the two sites is fundamentally different. At 120 km west (Fig. 5A), the birds vanish randomly or nearly randomly (mean LMV = 0.44) but sometimes with a slight tendency to go in the opposite direction from home (mean HDC = −0.44), whereas at 143 km north (Fig. 5B), the birds always vanish nonrandomly and consistently show very little scatter in their bearings (mean LMV = 0.81) but the mean vector is always oriented considerably west of the true home direction (mean HDC = 0.39).

Some re-analysis of Schmidt-Koenig's data in terms of homeward directedness of the mean vector and scatter of the bearings is possible. Thus, for example, if we look at the original data of Schmidt-Koenig (1966, page 41) from which Wallraff (1967, page 340) graphed the homeward component of Schmidt-Koenig's releases from the west, we discover that the nearly identical values for the homeward component shown for the releases at 30 km and 40 km in Wallraff's curve result from very different behavior on the part of the pigeons. The homeward component of 0.06 for 30 km is the average of the values (+0.64 and −0.51) for two releases both of which had bearings that were distributed nonrandomly ($P \leq 0.01$) but in which the mean vectors were oriented in nearly opposite directions, one homeward and one away from home. By contrast, the homeward component

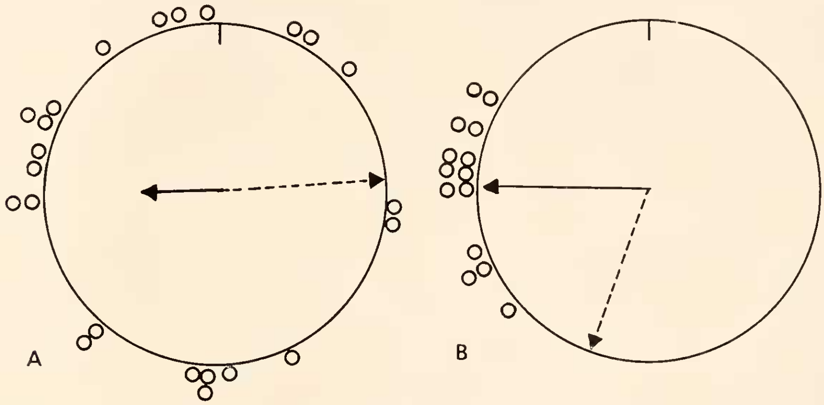


FIGURE 5. Release (A) showing very great scatter of the vanishing bearings, contrasted with a release (B) with little scatter but a mean deviating by a large angle from the home direction; A, Jersey Hill Fire Tower, New York, 74.5 miles from the loft, August 2, 1968, home bearing 85°, mean bearing 269° (random, $P = 0.287$); B, Castor Hill Fire Tower, New York, 89.1 miles, July 31, 1969, home bearing 200°, mean bearing 272° (nonrandom, $P = 0.0005$).

of 0.04 for 40 km is the average of the values (+0.23 and −0.14) for two releases both of which yielded random bearings. Thus emphasis on the homeward component has resulted in lumping together as similar examples of poor homeward orientation at intermediate distances values resulting from fundamentally different behavior. (Values for distances and for homeward components mentioned here are estimated from Schmidt-Koenig's (1966) figure and are thus only approximate.)

Wallraff's (1967, page 341) graph of distance effect in his own first-flight pigeons permits re-analysis in terms of homeward directedness of the mean vector and scatter of bearings. The results indicate that his data do not support the idea that *orientation* improves with distance. Thus his graph of releases from the east shows a rising homeward component at distances beyond 20 km, but this "improvement" turns out to be due largely to increased scatter in the bearings rather than to a more homeward-directed mean vector. In all but the first of his east releases, the mean vector is oriented away from home, hence the increasing scatter of his birds' bearings with distance results in a higher real value (but lower absolute value) for the homeward component. In short, there seems to be a trend toward randomness rather than toward improved homeward orientation.

The values for the homeward component obtained at one release site may differ significantly from those obtained at another site located approximately the same distance and direction from the home loft. For example, the mean homeward component at our 14.9 km east site (Fig. 1B) is 0.79, indicating very good homeward orientation. After conducting a series of five releases at this site (where the home direction is 247°), we performed a series of five releases at an alternate site 15.1 km east of the loft (home direction, 276°), and obtained a mean homeward component of 0.37, indicating much poorer orientation. Clearly the shape of the homeward component curve shown in Figure 2B would be quite different if the results at this alternate site were substituted for those at our usual site. The homeward component appears to depend upon peculiarities of the individual release sites that are not correlated with distance from the loft. Depending upon ones selection of sites, curves of many different shapes could be obtained when the homeward component is graphed as a function of distance.

It follows from this type of analysis that the homeward component is not a very useful basis for comparing pigeons' orientational behavior at different release sites. Much more meaningful information is provided by the combination of the homeward directional component and the length of the mean vector. However, our data indicate that neither of these varies consistently for our birds with the distance of the release site from the loft. Graue (1970) has recently also failed to find a distance effect in the orientation of his birds in Ohio. The distance effect does not appear to be a general phenomenon, and hence its theoretical implications are doubtful.

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Summary

1. Matthews (1955, 1963), Schmidt-Koenig (1964, 1966, 1968), and Wallraff (1967) have reported that pigeons orient toward home best when released close to the loft or at a long distance from it; they report poor orientation at intermediate distances, and suggest that this has important implications for the nature of the navigational system used by birds.

2. We have failed to detect any such distance effect in 172 test releases utilizing 2525 single-tossed pigeons from the Cornell lofts. When the homeward component is plotted against distance, we obtain dissimilar curves for the four cardinal directions. Furthermore, the values of the homeward component may be quite different at two release sites approximately the same distance and direction from the loft.

3. We obtained particularly good orientation at the intermediate distances where, according to the distance effect, it should be poorest. This was true not only of experienced birds but also of first-flight youngsters.

4. Analysis of our data, as well as re-analysis of some of the published data of others, indicates that a much clearer picture of the behavior of the birds is given by the combination of the homeward directional component and the length of the mean vector. This permits segregation of the two factors that together determine the homeward component. These two measures vary independently, and neither shows the distance effect.

5. I conclude that the distance effect is not a general phenomenon.

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Note Added in Proof

While this paper was in press, Wallraff (1970, *Z. Tierpsychol.,* **27**: 303–351) published an analysis of his data in terms of the accuracy of the mean bearing and the length of the mean vector (see his page 340). Also, Schmidt-Koenig (1970, *Z. Vergl. Physiol.,* **68**: 39–48) has published further data from his studies of distance effect in Germany. Although he continues to report a distance effect in the homeward component, he does not find the same effect in either vanishing interval or, more importantly, homing speed. This suggests that his birds released at intermediate distances are correcting their bearings soon after being lost from sight, while they are still within the "zone of disorientation." If this is so, it contradicts the hypothesis that the birds must be either close to home or very distant from home to orient accurately.